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INHERITANCE IN CREPIS CAPILLARIS (L.) WALLR. III.[2]

NINETEEN MORPHOLOGICAL AND THREE PHYSIOLOGICAL CHARACTERS[1]

BY
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INTRODUCTION

For several years variations in *Crepis capillaris* have been studied genetically. The study was commenced[2] in the hope of being able to determine whether the extensions of the Mendelian theory of heredity which were based on breeding data from *Drosophila melanogaster* would hold for higher plants. For this purpose it was necessary to know the mode of inheritance of a number of characters. This paper is concerned with the description and mode of inheritance of a number of variations found in *Crepis capillaris* (L.) Wallr.

It is evident that the material chosen for such a purpose should show variation of a hereditary nature and should also contain a low number of chromosomes. *Crepis capillaris* seemed to fulfil these requirements, for its chromosome number, 3 pairs, is the lowest reported for the higher plants, and the species is known as a variable one.

Linkage has been demonstrated in a number of plants and in some of the higher animals. Unfortunately, the chromosome number in those species in which linkage has been observed is relatively high, and in no case is the number of groups of linked genes equal to the haploid number of the chromosomes.

[1] This is a report on a part of a project supported by appropriations from the Adams Fund.

[2] Studies commenced by Professor E. B. Babcock in 1915 and carried on by the writer under his direction since 1918; published as nos. 6 and 7 of vol. 2 in the present series.

Material and Methods

The genus *Crepis,* containing over 150 species, is a member of the Cichorieae or chicory tribe of the Compositae, the best known related genera being *Hieracium, Lactuca, Sonchus,* and *Taraxacum.*

Crepis capillaris (L.) Wallr. is an annual, but under certain circumstances may assume the biennial habit. The plant first produces a rosette of radical leaves which have been found to vary in different plants from entire to bipinnately compound. The stem is usually single with paniculate branching above and varies from a few inches to four feet in height, largely depending upon conditions of growth. The cauline leaves are sessile, amplexicaul, clasping, the lower ones more or less lobed or pinnatifid, while the upper ones are slender and entire. The underside of the midribs of the rosette leaves, and to some extent the upper side, and the lower cauline leaves are more or less covered with bristly hairs. In many, but not all, plants the involucre and peduncle are glandular pubescent in addition to the fine gray tomentum which is always present. The brown terete achenes vary in length from 2 to 3 mm., are attenuate at both apex and base, and usually 10-ribbed. The yellow flower heads vary from 17 to 25 mm. in diameter.

During the course of the investigations, achenes of *C. capillaris* have been obtained from many localities of the temperate and subtropical zones of both the old and the new world. The species is apparently a native of Europe, but is now disseminated throughout the world.

The methods used in growing experimental cultures of *Crepis* have been previously published (Collins, 1922).

In presenting data from hybrid populations, the degree of correspondence of observed with calculated distribution has been determined by use of tables of probable errors of Mendelian ratios prepared by the Department of Plant Breeding of Cornell University. In the case of some dihybrid populations the method suggested by Harris (1912) has been used. This formula is $X^2 = \Sigma \frac{(o - c)^2}{c}$, in which o is the observed frequency of any class, c, the calculated frequency for that class, and Σ indicates that all the values of the type $\frac{(o - c)^2}{c}$ are added together. From Elderton's[3] tables for calculating the goodness of fit, the probability for the chance occurrence of the deviations in the observed classes has been obtained from the calculated value of X^2.

[3] Given in Pearson, K., *Tables for Statisticians and Biometricians,* Cambridge Univ. Press, 1914.

VARIATIONS IN CREPIS CAPILLARIS

Observations upon cultures grown from the achenes obtained from localities in many different regions have resulted in the discovery of a number of variations. Those which have been studied sufficiently to show their method of inheritance are described below. In assigning symbols to serve as genetic representatives of particular characters, the system in general use has been followed, namely, the use of the initial letter (or letters) of the name given to the character, small letters indicating a recessive, and capital letters a dominant condition.

BALD (b)

On August 17, 1918, a single plant ($19.18P_{23}$) in a culture of 47 plants grown from achenes sent from Copenhagen was found to be devoid of glandular pubescence on the involucre and peduncle. This variation has been named 'bald.' The second instance of this variation was in the same race but appeared only after two generations of inbreeding. Bald plants later appeared in cultures from other localities as follows: Sweden, England, France, Chile, and the Azores. It was of importance to know whether the same or different genes were responsible for the appearance of 'bald' in cultures from such widely separated sources. This could be determined by crossing the different races. If a single gene were involved, then bald F_1 plants should result, while if, on the other hand, glandular plants resulted in the F_1, this variation appearing in the different stocks would be the similar expression of different genes. As is shown in table 1, the same gene is present in each case.

TABLE 1

THE F_1 RESULTS OF CROSSING DIFFERENT GEOGRAPHICAL RACES OF BALD

Culture No.	Character of F_1		Total
	Bald	Glandular	
F_2 Copenhagen × Sweden (20.130) × Chile (21.23)	9	0	9
Sweden (19.235) × Cambridge (19.66)	4	0	4
Copenhagen (18.75) × Sweden (19.235) (19.H1, 20.57-8, 21.101)	56	0	56
Chile (20.36) × Azores (20.40), (21.25)	1	0	1
Sweden (19.H3) × Azores (20.40), (21.117)	7	5	12

In the last item in table 1 both bald and glandular plants are recorded. This is as it should be, for the 19.H3 plant was an F_1 glandular plant produced by crossing the Swedish bald race (19.235) with a Eureka glandular race (19.224). If the bald gene in the

TABLE 2

F_1 Results from Crosses of BB × bb

Pedigree No.	Character of F_1 plants	
	Glandular (B)	Bald (b)
19.H3	2	0
20.59	10	1
21.21	7	2
21.28	7	0
Total	26	3
Expected 1:0	29	0

TABLE 3

Back Crosses of the F_1 Bb to bb

Pedigree No.	Progeny segregation	
	B	b
21.17	7	3
21.18	5	6
21.19	6	7
21.24	4	2
21.117	12	13
21.126	4	2
Total	39	38
Calculated 1:1	38.5	38.5
Deviation	0.5 ± 3.84	

cultures from Sweden and from the Azores were identical, we should expect to obtain from such a back cross 50 per cent glandular and 50 per cent bald plants. The 5 to 7 segregation obtained is a close approximation to the expected 1 to 1 ratio. While the Copenhagen race has not been crossed with the Cambridge race, nor the Chilean

race with any except that from the Azores, we have evidence of their identity, since they have each been crossed with the Swedish race, which in turn was proved to be identical with the others. The bald plants from France have not been tested. Bald is inherited as a simple monohybrid recessive, as is shown by the results obtained from crossing with glandular plants. Table 2 presents F_1 data from crosses of bald $\times$ glandular. The one bald plant in culture 20.59 probably resulted from the failure to remove a single pollen grain during emasculation and represents an error in technique. The two bald

TABLE 4

F_2 Results from the Cross BB $\times$ bb

Pedigree No.	Progeny segregation	
	B	b
20.59	10	1
20.60	2	3
20.141	56	17
20.142	16	7
20.118	74	23
Total	158	51
Calculated 3:1	156.75	52.25
Deviation	1.25 ± 4.22	

plants in culture 21.21 may be ascribed to this same cause or to errors at time of transplanting, since culture 21.23, containing only bald plants, grew adjacent to 21.21 in the flat before transplanting to the field.

Table 3 shows that 39 glandular to 38 bald plants were obtained when the F_1 (bald $\times$ glandular) were backcrossed to the recessive parent strain. The expected 1 to 1 ratio was therefore realized.

The results from F_2 cultures confirm the conclusion regarding a single recessive factor conditioning the appearance of bald. While in almost all cases involving bald the glandular hairs are completely absent, in culture 20.141 some plants appeared to be somewhat intermediate, inasmuch as they developed a few small scattered gland hairs on the involucre. They were easily distinguishable from glandular plants. In table 4 these intermediates have been classified as bald,

but in the original records they were designated as intermediates. If the culture 20.141, containing the intermediate-bald plants, is removed from the table, the remaining cultures give an exact ratio of 3 glandular to 1 bald; when the intermediates are classified as bald, the deviation from a 3 to 1 ratio is less than the probable error. The progeny of two bald and two glandular F_2 plants were grown. Both of the former gave, as expected, only bald offspring, while the two glandular F_2 plants produced both types in F_3.

The nature of the intermediate plants has not been definitely determined. The selfed progeny from one plant ($18.d1P_{76}$) gave a culture (20.55) of 18 bald, 3 intermediate, and 3 glandular plants. That they were not due to the incomplete dominance of the hybrid produced by crossing bald with glandular is certain, for in the F_1 cultures (table 2) all plants were fully glandular. Another intermediate bald plant ($22.153P_{18}$) produced 5 glandular and 5 bald plants from selfed seed but none that could be classified as intermediate.

SMOOTH MIDRIBS (s)

The midribs of the rosette leaves usually have a hairy pubescence. From sporadically appearing plants, races have been obtained which do not show these rib hairs; such plants have been designated as 'smooth' (s). The F_1 resulting from a cross between these two types of plants were all rib-haired, and in the F_2 there appeared 556 rib-haired to 40 smooth plants. This is approximately a 15 to 1 ratio and suggests the operation of two independent genes, each producing the same somatic effect.

Duplicate genes are by no means unknown, having been reported a number of times in the literature of genetics. If two independent genes were operating in the cultures 21.140 and 21.141, the F_1 of this same cross when backcrossed to smooth should give a 3S to 1s ratio and some F_3 populations should give a 3 to 1 segregation. Evidence from cultures of these two types has been obtained; the data from them together with data from other crosses involving this character are given in table 5. The F_3 culture 21.189 was grown from one plant of an F_2 culture containing 58 rib-haired and no smooth plants. Such a deviation is, however, only three times the probable error and may well be due to errors of random sampling. The culture F_1 19.H1 was originally made to determine the relation of the gene for bald of the English race of *Crepis* to that in the Danish race and

was the hybrid between these two races. The parent plant from the English race was smooth, while the parent from the Danish race had rib hairs.

TABLE 5

SHOWING F_2 AND F_3 RESULTS FROM THE CROSS SSS'S', SSs'S', AND SsS'S' WITH sss's'

Pedigree No.	Progeny segregation	
	S	s
F_2 21.140	237	17
F_2 21.141	319	23
F_3 22.189	189	9
Total	743	49
Calculated 15:1	742.5	49.5
Deviation	0.5 ± 4.59	
F_2 22.55	25	12
F_2 22.56	5	2
F_2 22.60	22	6
F_2 22.61	4	2
F_2 22.62	9	1
F_2 22.63	34	8
F_2 22.41	66	24
Total	165	55
Calculated 3:1	165	55
Deviation	0.0 ± 4.52	
Back cross 19.H1	55	17
Calculated 3:1	54	18
Deviation	1.0 ± 3.83	

The 3 to 1 ratio obtained in 19.H1 indicates that the rib-haired ♀ used was heterozygous for the duplicate genes for rib hairs. This cross, as regards these characters, was a back cross of a heterozygote to the recessive parent, and constitutes additional evidence to substantiate the duplicate gene interpretation given above for the inheritance of rib hairs in these cultures.

LEAF VARIATIONS

From the very first acquaintance with *C. capillaris,* the different forms in the rosette leaves constituted the most striking and outstanding variations. They have proved equally as difficult to study genetically, due, first, to the difficulty in evaluating non-genetic variability resulting from age of plant and from environmental causes, and, second, to the complex heterozygotic nature of the material in the wild condition. Sears (1921) found in *Taraxacum* that the degree of leaf dissection is correlated with the age of a given rosette. The leaves of a very young rosette are almost entire, becoming progressively more dissected as the rosette becomes older. Stork (1920), also working with *Taraxacum,* found that in very young plants the rosette leaves ranged in form from entire to deeply pinnatifid-runcinate, but became *more, instead of less uniform,* as they grew older. Neither condition can therefore be taken as typical for that species. In *Crepis,* a closely related genus, there is a more regular sequence of development of leaf shape for a particular rosette. The juvenile leaves are usually entire or nearly so, and assume their typical forms gradually as the plant reaches the mature rosette stage just preceding the appearance of the flowering stalk. At this time there exist individual differences which range in form from entire to deeply pinnatifid or compound pinnatifid. That these differences are genetic is shown, first, by the fact that inbreeding has resulted in the isolation of races of the different types which breed true when grown side by side under similar conditions, thus to a large degree eliminating the effect of the non-genetic factors, and, second, that the forms when crossed give a fairly uniform F_1 and segregate into the parental and F_1 forms in the second generation.

By means of inbreeding and selection, a number of distinctive, uniform races have been obtained in almost homozygous condition. A brief description of each is given below.

VIRIDIS

Plate 45, figure 1

This form was isolated in 1919 from the Eureka (California) stock. The rosettes are small, 4 to 10 inches in diameter. The leaves are deeply lobed or pinnately parted, and are lacking in anthocyanin.

The blade of the leaf is of a darker color than the midrib. The color of the blade is Ridgway's varleys green, 31′ m. The midrib is covered on both upper and lower surfaces with hairy pubescence. The lobes are usually widest at the base, often having a minor lobe attached to the proximal edge of the base of the major lobe. Attached to the midrib between the lobes is a narrow wing. The lobes are usually close together, with the terminal lobe slender and pointed.

H6 RACE

Plate 45, figure 2

The H6 race was isolated in 1919 from a Berkeley *Crepis* stock. The size of the rosettes is more variable than in viridis, the rosettes ranging from 8 to 12 inches in diameter. The leaves are pinnately and bipinnately lobed; the lobes are constricted at the base and rounded at the tip, and inclined to twist, so that the plane of the lobe is not in the same plane with the midrib. Anthocyanin is conspicuously present. There are no hairs on the midrib. The lobes, usually six in number, are widely spaced. The terminal lobe is large and blunt-tipped. The narrow wing on the midrib is crimped, presenting a ruffled effect. The wing and edges of the lobes contain a blackish purple coloring which appears very early in the development of the plant. The leaf color, according to Ridgway's Standard, is cedar green, 31m. The characters which make up this type are dominant, excepting smooth ribs, when crossed with viridis.

PALLID

Plate 45, figure 1

This race was obtained in 1919 by inbreeding in the same Eureka stock that produced the viridis race. The rosettes are from 6 to 10 inches in diameter. This race produces more leaves in the rosette than do the preceding races, giving the rosette a thick mat-like appearance. Pallid lacks anthocyanin and is a much paler green (Ridgway's forest green, 29′m.) than the two races described above. The lobes are broadest at the base, are set closely together, and have pronounced, pointed teeth. This race does not grow so rapidly as the darker green races. Rib hairs are present on the midrib.

SIMPLEX Z9

Plate 46, figure 1

Simplex Z9 was isolated in 1920 from a stock originating from seed collected at Quy Fen, England. The original culture consisted of plants ranging from entire to pinnatifid. The simplex Z9 race was obtained by inbreeding plants with entire leaves. Although inbreeding has reduced the amount of variation, there still appears in this supposedly homozygous race a small percentage of semi-pinnatifid-leaved plants (pl. 46, fig. 1). Anthocyanin and rib hairs are present.

SCALARIS e29

Plate 46, figure 2

This race was isolated in 1919 from the Eureka stock of *Crepis* which produced the viridis and the pallid races. It is characterized chiefly by long, simple, pinnately-divided leaves with pointed lobes. The terminal lobe is slender and elongated, often curved to one side near the tip. Both anthocyanin and rib hairs are present. The average number of lobes per leaf is 10. It is dominent when crossed with simplex Z9 or with viridis. Typical leaves of the scalaris e29 and the simplex Z9 races are shown in plate 52, together with the F_1 and F_2 types obtained when these two races are crossed. In the F_1 a few extreme variants occur which approach the simplex form, but the majority are more nearly like the scalaris and constitute a fairly uniform intermediate type. In the F_2, three types are distinguishable (see pl. 51, fig. 2), the two grandparental forms and an intermediate scalaris form similar to the F_1. When the intermediate-scalaris and the scalaris are grouped together a 3 to 1 ratio is obtained (see table 6).. The intermediate forms differ from the scalaris in having the lobes less deeply incised, some more so than others, but still classifiable as intermediate. (See third and fourth leaves in F_2, pl. 52.)

From the results of breeding it appears that there is present one main gene for lobing and that dominant modifying genes are involved which act cumulatively, thus producing intermediates of different grades of pinnate lobing. As a corollary to this hypothesis races breeding true for different grades of intermediate pinnatifid lobing should be possible. There is evidence that such races occur. Several intermediate forms have been tested and found to be fairly constant.

A race obtained from Seattle, Washington (named "Seattle") appears to be such a homozygous intermediate form.

Races of *Crepis capillaris* also differ in number of lobes per leaf and in length of leaf (Rau, 1923). The scalaris race shown in plate 52 has a large number of lobes. The two races differ, however, in length of leaf. The leaves of the scalaris parent shown in plate 52 are shorter, and of the simplex parent larger, than the mean size typical for each race. The F_1 is usually larger than either parent. The F_2 in the same figure shows the segregation for size which appears to be due to multiple genes.

The inheritance of pinnatifid and entire leaf forms in *capillaris* conforms in general to the type of inheritance of corresponding forms in a number of other plants. Rasmusen (1916) found in species crosses in grapes that differences in leaf form behaved in a very similar way. The F_1 appeared to be intermediate between the shapes of the parent leaves. In the F_2, a series was produced which included the grandparental forms, the F_1 type and different grades of intermediates. If the deeply toothed and intermediate toothed classes were grouped together, a ratio of 3 toothed to 1 non-toothed resulted.

Shull (1918) found four different leaf forms of the shepherd's purse to be caused by two pairs of factors. As in *Crepis,* the deeply pinnatifid forms were dominant. The plants were also subject to considerable fluctuating variation. Two races of *Urtica,* one having deeply serrated leaves, the other, leaves with entire edges, gave serrated leaves in F_1 and a ratio of 3 serrated to 1 entire leaf in the F_2 generation (Correns, 1912). In cotton, however, the deeply palmately parted leaf form is not dominant when crossed with the five-pointed upland type, but produces an intermediate type in F_1 with a ratio of 1:2:1 in the F_2 generation (Shoemaker, 1909). Kristofferson (1923) found that the difference in lobing of the leaves of two species of *Malva* was brought about through a single genetic factor, and resulted in a somewhat intermediate condition in F_1 and a 3 lobed to 1 non-lobed condition in the F_2, although considerable variation in the degree of lobing in the pinnatifid class was recognized. Tedin (1923), on the other hand, found that pinnatifid and entire leaved plants differed genetically by two factors.

TABLE 6

THE RESULTS FROM THE CROSS OF LEAF FORMS. Sc × sc

Pedigree No.	Progeny segregation	
	Sc	sc
21.140	177	75
22.7	99	24
22.10	50	17
22.14	14	6
22.17	48	15
22.19	92	19
22.22	167	52
22.24	51	14
22.25 .	37	13
22.26	29	2
Total	764	237
Calculated 3:1	750.75	250.25
Deviation	13.25 ± 9.24	

SCALARIS e28 (Sc)

Plate 47, figure 1

This pinnatifid leaf form was isolated in 1919; it originated from a single plant which was a sib to the one producing the scalaris e29 race. These two forms have much in common, but are different in size, e28 being smaller and not so vigorous as e29, and having shorter and blunter lobes.

Two races of the pinnatifid leaf forms isolated from the Berkeley (H6) race of plants and from the Eureka population (e28), respectively, differ in a number of minor characters, as shown in the following comparative list:

H6 (BERKELEY)	CHARACTERS	e28 (EUREKA)
dark green	color of leaf	dark green
dark green to blackish	color of midrib	light green
pronounced	anthocyanin	none or trace
pronounced	crimping of rib-wing	none
none	rib hairs	present
pronounced	black edge on leaf	trace only
blunt and rounded	terminal lobe	narrow—pointed
rounded	lateral lobe	slender—more pointed
wide (very)	lobe spacing	wide (medium)
pronounced	Constricted base of lobes	none or trace
large	secondary lobes	none

Plants of these two races when crossed showed almost the entire group of H6 characters (rib hairs excepted) in the F_1, while in F_2 (21.141) there appeared the parental types and in addition some composite types that showed some characters from each parent. When each character pair was considered separately, however, a peculiar situation was presented. Six of the character pairs gave 9 to 7 ratios, and a seventh pair, rib hairs vs. smooth ribs, gave a 15 to 1 ratio. The data for these characters are included in table 7. It is quite probable that these six character pairs as given are the result of not more than three sets of genes, since the two characters, black edging of the leaves and anthocyanin of the midribs, are both concerned with the distribution of anthocyanin pigment in the plant. The shape of the terminal and of the lateral lobes is probably conditioned by the same pairs of genes, while the crimping of the wing of the midrib and the constriction of the base of the lobes also probably result from the action of the same gene. The Berkeley plants were evidently homozygous for the dominant complementary genes of all three character couples. This genotype may be expressed as AA′BB′CC′, the simultaneous presence of both the primed and unprimed dominant genes being necessary to cause the development of the respective characters. The Eureka race would then have the genotype aa′bb′cc′ with respect to these characters.

TABLE 7

SEGREGATION OF SIX PAIRS OF CHARACTERS IN THE F_2 FROM THE CROSS H6 × SCALARIS e28. (CULTURE 21.141)

Segregation	Calculated 9 : 7	Deviation
162 black edge : 103 green edge	149.06 : 115.93	12.94 ± 5.45
166 anthocyanin : 109 none	154.71 : 120.33	11.29 ± 5.55
142 angular lobes : 112 round	143.1 : 111.3	1.1 ± 5.33
150 narrow lobes : 104 broad lobes	143.1 : 111.3	6.9 ± 5.33
135 constricted lobes : 118 non-constricted	143.1 : 111.3	8.1 ± 5.32
165 crimped wing : 101 flat wing	149.58 : 116.34	15.42 ± 5.49

REVOLUTE (r)

Plate 47, figure 2

This race appeared in 1919 among offspring of a plant of the Eureka stock, which had been self-pollinated. The plants are characterized by a definite downward curling of the edge of the leaf

toward the midrib. It occurs in both entire and pinnatifid types, though it is more conspicuous in the former. In appearance much like the *funifolia* mutant of *Oenothera Lamarckiana* described by Shull (1921), in which both rosette and cauline leaves have edges curled under. The knowledge of the genetic basis for this character has been obtained incidentally in experiments designed to show inheritance of other characters. The data thus obtained indicate that revoluteness is conditioned by complementary recessive genes.

TABLE 8

Showing the Segregation of Revolute Leaves in Two Cultures

Pedigree No.	Progeny segregation	
	R	r
19.e5	62	17
Calculated 3:1	59.25	19.75
Deviation	2.75 ± 2.60	
21.140	233	20
Calculated 15:1	237.19	15.81
Deviation	4.19 ± 2.60	

It is significant that revolute appeared only in these two cultures, which were derived from a common source, because it indicates that the genes were present in the wild plants from which the starting point of these cultures was obtained. The 15 to 1 ratio made its appearance in the sixth generation from the wild plants (some out-crossing occurs in this pedigree), while the 3 to 1 ratio appeared in the second generation.

BICEPHALIC (bi)

Plate 48, figure 1

This character designates a type of fasciation in which the buds are more or less joined together in twos. The peduncle is also frequently flattened. This variation was first found in 1920 on a single plant (20.30) which was grown from achenes obtained from Chile. This original plant was crossed with $20.130P_{19}$, which produced an F_1 culture of 9 normal plants. The F_2, consisting of 81 plants, segregated into 60 normal to 21 bicephalic, clearly a monofactorial ratio.

In no case were all the buds of a plant of the bicephalic kind. Some plants indeed produced only a few double buds. F_2 bicephalic plants of both types were selfed and F_3 cultures produced. The data from F_3 cultures are shown in table 9.

TABLE 9

TYPE OF PLANTS PRODUCED BY SELFING F_2 BICEPHALIC PLANTS

F_2 Plant No. 23.283	Progeny F_3	
	Bicephalic	Normal
*P_{68} +	6	1
P_{70} +	2	6
P_{96} +	8	0
P_2 ++	6	0
P_{10} ++	6	0
P_{23} ++	5	1
P_{24} ++	2	0
P_{30} ++	0	1
P_{44} ++	20	0
P_{46} ++	8	0
P_{48} ++	5	2
P_{57} ++	2	0
P_{81} ++	5	(2?)

* The single + indicates an F_2 plant on which but few bicephalic buds appeared. The ++ indicates plants having many such buds.

It appears that F_2 bicephalic plants breed true in F_3. Plant 70 which had only a few double buds, was apparently a heterozygote, for it gave a 3 to 1 ratio in F_3. The other F_3 plants listed as normal may have been genetically bicephalic, since they showed some evidences of fasciation in the stems and malformation of buds; but no doubling or cohesion of the buds was found.

ANTHOCYANIN

This pigment is distributed to many parts of the plant, but is most noticeable in the midribs of the leaves and on the lower portions of the stems. Culture 19.e8 segregated into 94 plants with anthocyanin to 39 with none or developed only to a slight degree. The ratio in this case is 2.82 to 1.17, in which the deviation is less than twice the probable error. This segregation can be considered only as suggestive because of the difficulty of accurately classifying this character

in *Crepis*. The appearance of purple anthocyanin color depends upon a certain amount of sunshine and exposure to light. Plants known to be capable of producing the color will show it to only a small degree if conditions for anthocyanin development are adverse, while, on the other hand, races in which it does not normally appear conspicuously will produce it under conditions of sudden exposure to direct sunshine or sometimes as a result of mutilation caused by animals or insects. The development of anthocyanin is a matter of degree, for the potentiality for its development is not entirely absent from any race so far obtained. In the viridis race we have it in its lowest and in the H6 race in its highest development. Crosses between high and low anthocyanin races (other than 19.e8 mentioned above) in general produced F_1 plants showing the darker anthocyanin of the H6 race, but in F_2 produced a series of forms showing a gradation in pigment from one parent to the other. In most cases the parental types were also duplicated. One such cross, H6 $\times$ viridis e33, gave an F_1 more nearly like the H6, but in F_2 the types were distributed as follows: 9 of H6, 3 of viridis, and 3 distinctly between these two parental types. The segregation of anthocyanin has been observed in other cultures (e26 = 3 to 1), but has not, in general, given sufficiently regular results to warrant the drawing of conclusions regarding its genetic basis. The analysis can only proceed when facilities are available to control more accurately the environmental factors which alter its development.

DWARF II (dII)

Plate 48, figure 2

This variation first appeared in culture 21.99, which was the second selfed generation from achenes obtained from Lyons, France. It is characterized by a very small rosette of slender semi-scalaris leaves which are blotched with yellow and yellowish red coloration, giving them the appearance of being about half-dead. Due to their peculiar appearance the first plants were thought to be suffering from poor environment, although adjacent plants were healthy. The plants when mature are very small (3–6 inches in height), the stems very fine and spreading. In the first culture the dwarf effect appeared to be recessive (5 dwarfs in 16 plants) and bred true in the next generation. Culture 22.159 from $21.99P_{7s}$, a normal plant, contained 51 plants, 3 of which were dwarf II and 3 somewhat dwarfish but not typical for dwarf II. This is approximately a 15 to 1 ratio, and

indicates that there may be duplicate genes for dwarf II; sufficient data are not at hand to establish the hypothesis. Culture 22.160 (from $21.99P_{15}$, a normal plant) gave 84 normal plants.

The yellow appearance of the leaves in dwarf II seems to be a dominant character from its appearance in 22.407, F_1 of the cross $22.169P_{22} \times 22.261P_4$, the male parent being a dwarf II plant from a pure culture. Inasmuch as the F_1 plants are not dwarfish, it appears that the yellowing and dwarfing may be due to separate but probably linked genes. All the dwarf II plants which have appeared were yellowish, and we may therefore assume that, instead of linkage, the appearance of dwarf II is dependent on the presence in the zygote of the dominant gene causing yellowing.

DWARF III (dIII)

Plate 49, figure 1

This variation first appeared in 1919 culture e5. It reappeared in 1921 in a culture (21.76) which came from the same source as e5. The ratio of normal to dwarf III in 21.76 was 15 to 1, and in the progeny of $21.76P_1$ (culture 22.117) 3 to 1. (See table 10 for data.) Dwarf III was at first called 'semi-lethal,' because of the high mortality in this class of plants. These plants remain very much smaller than their normal sibs during the rosette stage and reach maturity much later. A large percentage die after they have formed a rosette and before they reach the flowering stage.

This variation appeared in several members of the same stock which produced revolute, viridis, and pallid.

SPREADING (sp)

Plate 49, figure 2

A lax, open-branching habit which appeared in 20.37, the French stock of *Crepis*. The stems and branches are long and slender, appearing to be so weak they cannot support themselves in upright position. Dwarf II appeared in this race and all have this spreading habit. Data from crosses (21.26 and 22.173, table 10) show that it is a recessive character. When the same plant ($20.37P_3$) was crossed to another erect plant ($19.H1P_{11}$), it behaved as a dominant (21.28, 22.41, and 22.43, table 10). Of the F_2 cultures, only 22.173 was grown under desirable conditions; the others were overcrowded in greenhouse and lath house, which interfered with proper development of this character.

PROCUMBENT (p)

This variation is similar in appearance to spreading. It first appeared in culture 20.40, which came from achenes sent from the Azores Islands. Unlike spreading, it seems to be dominant, the F_1 plants, 21.28 (from $20.40P_9 \times 20.111P_4$), being of the procumbent type. The F_2 cultures were grown under crowded and unfavorable

TABLE 10

Segregation of Plant Characters

Culture No.	Segregation	
	Normal	Variant
21.76	57	4 dwarf III
Calculated 15:1	57.19	3.81
Deviation	0.19 ± 1.28	
22.159	48	3 dwarf II
Calculated 15:1	47.81	3.19
Deviation	0.19 ± 1.17	
22.117	12	4 dwarf III
Calculated 3:1	12	4
Deviation	0.0 ± 1.17	
22.99	11	5 dwarf II
Calculated 3:1	12	4
Deviation	1.0 ± 1.17	
22.173	70 erect	26 spreading
Calculated 3:1	72 erect	24 spreading
Deviation	2.0 ± 2.86	
22.41	18	39 spreading
22.43	5	15 spreading
	—	—
Total	23	54
Calculated 1:3	19.2	57.8
Deviation	3.8 ± 2.56	

conditions which made accurate classification difficult and uncertain. One F_2 gave a 1 to 1 ratio and another the ratio 2 procumbent to 1 normal.

ERECT (e)

Plate 50, figure 1

A strain characterized by erect habit of growth, large stiff lateral branches, and a thick rigid central axis. The branches make an acute angle with the axis, the whole plant having the form of an inverted cone. This form was selected from the F_2 of a cross between the Danish and Swedish stocks.

PALEA (p)

Plate 51, figure 1

The nature of this character has previously been discussed (Collins, 1921). It originally appeared in an F_1 hybrid and was considered a reversion to a possible, pre-composite, ancestral condition. It has appeared in every case in hybrids, never in inbred races, and was probably introduced with the Danish stock, since the same plant ($17.198P_2$) of that stock is in the pedigree of all the hybrids which have produced palea. Races homozygous for palea have been obtained. Preliminary data show palea to be conditioned by a single recessive gene.

Linkage

In a species having only three pairs of chromosomes, it would seem fairly easy to establish groups of linked genes, especially when the species was known to be more or less polymorphic. However, it has not yet been possible to realize this end, due to the unexpected relations of some of the genes in this species. For instance, there are four cases of complementary recessive genes, and three characters dependent upon duplicate dominant genes. The determination of linkage groups under such conditions is complicated because it requires a longer time to obtain races with a known and tested genotype.

The gene for bald involucre appears from data in tables 12 and 13 not to be linked with the gene for smooth ribs nor with the gene for procumbent, since the ratios show independent segregation.

It is of course obvious that linkage must occur between one pair of complementary genes for smooth ribs and one pair of complementary genes for revolute leaves, since there are four pairs of genes and

only three pairs of chromosomes. A cross involving these two characters gave the following results (+ indicates the presence and — the absence of the character named):

TABLE 11

DIHYBRID SEGREGATION OF SMOOTH × REVOLUTE IN A CULTURE WHICH GAVE A 15:1 RATIO FOR EACH CHARACTER SEPARATELY

Culture 21.140	Smooth ribs Revolute leaves	− −	− +	+ −	+ +	Total
	Observed	202	16	32	2	252
	Calculated 57 : 3 : 3 : 1 :	224	11.79	11.79	3.93	252
	$\frac{(o-c)^2}{c}$	1.98	1.50	34.64	0.12	$X^2 = 38.24$ $P = .0000$

The calculated numbers agree fairly well with those obtained except in the third class where the observed numbers are more than twice as large as the calculated number. This class may have been increased at the expense of the first class by placing in it some plants which genetically belonged in the latter. The observed number in the first class is considerably less than the calculated number for that class. These figures indicate that the genes are arranged in the three pairs of chromosomes as follows: R, s,—(R′S′) (r′s′)—r, S, where primed genes are the complements of the unprimed genes. Were the linkages as follows (R′s) and (r′S), the F_2 population should consist of three classes in the proportion of 14:1:1, assuming that little or no crossing over occurs. A high percentage of crossing over in the latter type of linkage would give approximately the results obtained. It appears, therefore, that either the dominants are linked, as stated above, or that there is a high percentage of crossing over between the linked genes. This inference can be tested experimentally, for races have been obtained which gave 3 to 1 ratios for both of the characters.

EFFECTS OF INBREEDING

The flowers of *Crepis* are perfect and, although self-fertilization can take place, the arrangement of the stigmas in respect to the stamens is such as to permit cross-pollination before self-pollination can be naturally effected. The stamens are united into a tube surrounding the style, and the pollen is shed on the inside of this tube.

TABLE 12

F_2 Results from the Dihybrid Cross, Glandular and Hairy Midrib × Bald and Smooth Ribs, Showing Independent Segregation

Culture 22.41*	Observed segregation	Calculated segregation 9 : 3 : 3 : 1	$\frac{(o-c)^2}{c}$
Glandular and Rib Hairs	36	41.01	0.61
Glandular and Smooth	11	13.68	0.52
Bald and Rib Hairs	20	13.68	2.84
Bald and Smooth	6	4.56	0.42
	73	72.96	$X^2 = 4.39$ P = 0.2264

*Rib hairs vs. smooth in this culture show a 3 : 1 ratio.

TABLE 13

Showing Independent Segregation in F_2 of Dihybrid Cross, Glandular-Erect × Bald-Procumbent

Culture No. 22.41	Observed segregation	Calculated segregation 9 : 3 : 3 : 1	$\frac{(o-c)^2}{c}$
Glandular—procumbent	17	20.25	0.37
Glandular—erect	10	6.75	1.56
Bald—procumbent	7	6.75	0.01
Bald—erect	2	2.25	0.03
	36	36.00	$X^2 = 1.97$ P = .5773

The style is bifid with the stigmatic surface on the adjacent faces of the lobes. With the beginning of anthesis the style elongates, pushing the upper end out from the stamen tube and sweeping the pollen out with it on its outer surface. The stigmatic lobes then separate and assume a position at right angles to the style. The pollen at this stage is below the receptive surface of the stigma, which is, however, exposed to insects, the means by which cross-pollination is effected. Later the stigma lobes curl into a short spiral which brings the receptive surface of the stigma in contact with its own pollen or that of an adjacent floret of the same head. Under natural conditions *Crepis* is often cross-pollinated by insects, and this preserves a heterozygosity of the germinal material. A similarity of the effects of continued inbreeding in *Crepis* to the effects of inbreeding in maize has been noted (Collins, 1920). It was shown that inbreeding caused a reduction in the size of the plants and increased the length of the vegetative period. Other data are now available which show in another way the general heterozygosity of *Crepis capillaris* as it occurs in a wild state. Thus the seed collected from a few wild plants near Eureka, California, has been the source of the following races: viridis, scalaris-e28, pallid, and revolute (leaf form variations); of three types of partial albinos (chlorophyll development); and of the variations, dwarf III and fasciation (the plant as a whole). From the Berkeley wild plants we have obtained plants with smooth ribs and the leaf form H6; from England, the leaf form simplex-Z9; from France, dwarf II, spreading, chlorina, and tubular flowers. Palea probably came from the Danish material. As mentioned in another section, bald has appeared independently in the cultures from six different geographical regions. The Eureka stock has produced the greater number of new races. This is not taken to mean that it is necessarily more heterozygous but that many more plants from this source have been under observation. We have presented here an instance of a remarkable germinal diversity in locally developed strains of a single species. Although many of the characters appeared only after hybridization between local races or stocks, the evidence does not, except in a few cases, show these characters to be due to complementary factors. The appearance of bald from such widely separated localities as Chile and Sweden and from other less widely separated localities is of particular interest, for it shows that either a certain locus of the germinal material mutates more readily than others or that all these local races have originated from a single stock

in which this gene was present; the former is, however, more probable, for it has been shown in *Drosophila* (Sturtevant, 1921) that certain loci are more mutable than others. Additional evidence that this is the case is found in the fact that a similar variation, bald, has been found to occur in at least four other species, *C. bursifolia, C. biennis, C. aspera,* and *C. dioscoridis.* A similar germinal diversity among local races of *Drosophila melanogaster* from equally widely separated localities has not been found, and Sturtevant suggests that this may be due to a frequent transportation of individuals from one locality to another. The chances are probably as great for transportation of *Crepis* seeds along with agricultural seeds as for the transportation of *Drosophila* among fruits.

It is possible that some of these variations might have arisen from mutations occurring in the cultures under observation. A study of the wild plants in the fields about Eureka, however, disclosed the fact that some of the forms obtained in the greenhouse by inbreeding were also appearing there among wild plants. In this material it is impossible to say whether any new recessive variation appeared as the result of a recent gene mutation or the segregation of a recessive from a heterozygous parent stock.

Variations in Chlorophyll

A number of different variations involving a loss of chlorophyll have appeared. These variations are evident in the seedling stage, but, unlike the usual albinic condition in seedling plants, most of these albino types develop sufficient chlorophyll as the plant grows to enable the plant to live. One type of pure white seedling always dies in the seedling stage. The other types are either pure yellow or yellowish green. The percentage of seedling mortality in these classes is higher than in pure green seedlings.

A complete analysis of the genetic relations of these different types has not yet been possible, but a sufficient study has been made to warrant a preliminary report in this general account of variations in *Crepis capillaris.*

CHLORINA (C)

Chlorina signifies a chlorophyll deficiency in seedling and mature plants. The middle portion of the leaves of chlorina plants is yellowish, but both tip and base contain more or less chlorophyll and thus it is possible for the plant to function. This character first appeared

in culture 21.99. In 1922 a culture of six chlorina plants was obtained. When these chlorina plants were crossed with normal green plants, the two classes of plants—normal and chlorina—appeared in the progeny in equal numbers, thus indicating that the chlorina plants were heterozygous for green. Self-fertilization of the green resulted in only green progeny. The seedling progeny from self-fertilized chlorina plants consisted of three classes: pure yellow, pale green, and normal green, in the ratio 1 to 2 to 1. The yellow seedlings died, the pale green ones developed into chlorina plants, and the green seedlings produced only green plants. The gene for chlorina is therefore dominant and has a lethal action when homozygous.

TABLE 14

SEGREGATION OF SEEDLING PROGENY OF SELF-FERTILIZED CHLORINA PLANTS

Culture No.	Green	Pale green	Yellow
24.171	46	60	26
24.173	13	17	6
24.174	66	?	33
Total	125	77	65
Observed	202		65
Calculated 3:1	200.25		66.75
Deviation	1.25±4.77		

In table 14 the seedlings in culture 24.174 intergraded in such a way that it was impossible to make an accurate segregation of pale green from green; consequently the two classes are combined in the table. Separation of the two green types in other cultures was less difficult, although it is apparent that some pale green plants have been included in the green class.

GOLDEN YELLOW (y)

The type known as golden yellow behaves as a monohybrid recessive as shown by data in table 15.

These golden yellow seedlings gradually develop chlorophyll and finally reach maturity, although growing much more slowly than their green sibs. These plants can, however, be distinguished in the mature stage, due both to size and to the peculiar distribution of the chlorophyll. They produce mature rosettes that show a mottling

of yellow and green through the leaves, which looks much like the plant disease known as 'mosaic,' or rosettes on which the central and thus younger leaves of the plant are a clear yellow. These yellow leaves later develop chlorophyll and become normally green.

It would appear from table 15 that the golden yellows would be homozygous recessives; but this is not the case, for the seedlings from selfed 'yellow center' and from 'mottled' plants show some of them to be heterozygotes. Only one plant has yet been found which was homozygous for yellow.

TABLE 15

MONOHYBRID SEGREGATION OF GOLDEN YELLOW IN THE PROGENY OF GREEN PLANTS

Culture No. 1921	Progeny segregation of seedlings	
	Green	Yellow
$177P_{13}$	10	3
$177P_{16}$	12	3
$177P_{17}$	278	84
$177P_{38}$	13	5
$177P_{40}$	15	3
$177P_{78}$	36	10
$177P_{124}$	23	6
Total	387	114
Calculated 3:1	375.75	125.25
Deviation	11.25 ± 6.54	

That there are other genes which also produce yellow seedlings is evident from table 16. The three plants P_{39}, $_{66}$, and $_{76}$ were green as seedlings and normal green in the mature stage. They apparently were heterozygous for two recessive genes which produced the same or a very similar type of yellow. The progeny of P_{25} indicate still another type of yellow indistinguishable phenotypically from those already mentioned. Here the production of chlorophyll in the seedling stage is dependent on the simultaneous presence of two dominant genes, and the absence of either one results in a yellow type of seedling.

Trow (1916) reports a similar case of complementary recessive genes in the production of albino seedlings in *Senecio,* another genus of the Compositae.

TABLE 16

Showing Seedling Segregation in the Progeny of Green Plants Indicating Complementary Recessive Genes for Golden Yellow and Duplicate Genes for Chlorophyll

Culture No.	Progeny segregation of seedlings	
	Green	Yellow
$21.177P_{39}$	44	3
$21.177P_{66}$	13	1
$22.177P_{76}$	45	3
Total	102	7
Calculated 15:1	102.19	6.81
Deviation	0.19 ± 1.70	
$21.177P_{25}$	22	13
Calculated 9:7	19.687	15.312
Deviation	2.312 ± 1.98	

VIRESCENT YELLOW (v)

A third type of seedling called virescent yellow has a small amount of green color in addition to the yellow. These seedlings, like the yellow ones, may produce two types of mature plants, namely, pure green plants and green plants with pale green younger leaves at the center of the rosette. The data at present indicate that virescent plants are produced when a gene dominant to yellow but recessive to green is present with the gene for yellow, which changes yellow seedlings to virescent and yellow-center rosettes to pale green centers. When virescent plants are selfed, then green, virescent, and yellow are obtained, but no virescent plants have appeared in the progeny of yellow plants.

It is hoped that in another place it will be possible to publish more extensive data and a complete discussion of the inheritance of chlorophyll deficient characters in *Crepis* which cannot be given at this time.

GENERAL DISCUSSION

In order to establish and preserve true breeding strains of the different types observed in the cultures, type plants were self-pollinated in successive generations. This most intense type of inbreeding affected these cultures in very much the same way as inbreeding has affected maize. Reduction in size and a slower rate of growth were the most noticeable results of inbreeding together with a slight increase in sterility. Most of the experiments to show the effect of inbreeding in plants have been with domesticated forms in which it is possible to have a genotypic constitution that might not exist in a wild state, because characteristics which would unfit the individual for survival in natural conditions are often preserved under the artificial conditions of cultivation. The inference is that wild species would differ in fewer genes than their cultivated relatives. However, the inbreeding experiments on *Drosophila* (Castle, 1906) produced no bad effects. Collins (1919) states that self-fertilization in teosinte, a wild relative of maize, causes no loss of vigor such as is known to occur in maize. On the other hand, Darwin (1876) concluded that wild species which are naturally cross-pollinated are, on the whole, adversely affected by inbreeding. It appears then that the results of inbreeding any race, cultivated or wild, would be an index to its genotypic heterozygosity or homozygosity. With this as a criterion, there is indicated a condition of germinal heterozygosity in *Crepis capillaris*. There appears to be a certain similarity between wild heterozygous species of *Crepis* and the cultivated races of maize in the type of recessive genes which persist in the genotype. In maize, a number of genes are present which produce characters that are so abnormal (sterility, extreme dwarfs, albinos) that they are propagated only with difficulty and would seldom be found under natural conditions. Examples of similar forms have appeared in inbred strains of *Crepis*. It may therefore be considered that natural selection has not eliminated these genes from the germinal material of the wild species. The genes in *Crepis* which affect vigor also produce results comparable to similarly acting genes in maize.

Evidence of the genotypic heterozygosity of *capillaris* has also been gained from another source. Seeds have been obtained from widely separated localities and grown side by side in the greenhouse

and garden. The number of different forms resulting either in the first or later generations and as a result of controlled cross-pollinations show that the germinal material was indeed far from homozygous. It is of importance, because of some current theories regarding the influence of the habitat upon the genotype of a local species (Turesson, 1922), to observe the behavior of these various forms when grown in as nearly identical conditions as can ordinarily be furnished in a greenhouse or garden. Plants belonging to many different genera were collected by Turesson from contrasted habitat localities in Sweden and grown together in a common garden. He found that in general each particular type of a species found in each of several different habitats maintained its characteristics in the absence of the habitat to which it seemed especially modified. He sees in such phenomena a refutation of the theory, now generally held, that the form predominating in a given locality occurred as a chance mutation or recombination and was preserved through natural selection. The theory substituted for this is Lamarckianism expressed in modern terminology, namely, habitat causes a change in the fundamental genotype of the species such that a phenotype is developed which permits the plant to flourish in a specialized habitat. His report deals principally with three types of plants in all his species, viz., dwarf forms, upright or erect forms, and spreading or procumbent forms, each of which was found in a location favorable to the existence of that type while unfavorable to the other types; and each thus becomes a demonstration of the effects of natural selection. In our study of *Crepis* forms we have not been fortunate enough to study wild populations of *Crepis* in all of the localities from which we have obtained seed, but we have produced hereditary strains of erect forms, spreading forms, and dwarf forms from the same habitat at Eureka, a fact which does not especially favor the existence of any one type. Dwarf forms have also appeared in cultures from other places (France and Denmark), whose definite habitat characteristics are unknown to us. Similar plant forms are well known to occur sporadically in many wild and domesticated species. Mutations giving rise to prostrate and dwarf types in plants are not infrequent when compared to other types of change. If we accept the idea of a *genotypic response* of the species to the habitat, are we not also admitting the inconstancy of the gene, a theory which is no longer tenable? Continuing the assumption, it is not clear why these different hereditary types, such as we have in *Crepis,* remain constant in a single unvarying habitat.

The very fact that they do not approach a common type under cultivated conditions supports the theory of the constancy of the gene and is evidence of the inability of the habitat to induce genotypic changes.

The occurrence of duplicate genes in other plants has brought forth the opinion that they may indicate the presence of duplicated chromosomes. Three cases of duplicate genes have been found in *Bursa* (Shull, 1920), a plant having 32 chromosomes (4×8), while a case of triplicate genes is reported in a wheat (Nilsson-Ehle, 1909) which has 42 chromosomes. This number is three times the number (14) found in several species of *Triticum* (Sax, 1921). Several pairs of duplicate genes have been found in *Crepis capillaris*. No plants producing such ratios have been examined cytologically, but in no visible way do they differ from plants which give 3 to 1 ratios for the same characters. From what is known regarding the effect of duplication of single chromosomes or of whole sets of chromosomes in *Datura* (Blakeslee, 1922) and in *Nicotiana* (Clausen and Goodspeed, 1924), it is difficult to suppose duplication of chromosomes has occurred here. That we have parallel mutations in identical loci of two chromosomes of the same kind derived from a form with a different number by some meiotic irregularity is equally improbable, for *capillaris* has but three pairs of chromosomes, no two similar enough in size to be construed as duplicates. There are several other ways to account for the appearance of duplicate genes, some of which have been discussed by Shull (1918). Four of these possibilities are (*a*) the occurrence of similar gene mutations in different chromosome pairs; (*b*) the mating of non-homologous chromosomes; (*c*) duplication of entire chromosomes; and (*d*) duplication of sections of chromosomes. The possibility of a chromosomal duplication as the cause of the origin of duplicate genes in *Crepis* is very unlikely, as has been shown above. The other possibilities cannot be dealt with so readily. It would appear, however, that, had duplication of a section of a chromosome taken place, other characters, the genes for which were located in the duplicated section, should show similar inheritance ratios. As a matter of fact, two other characters in *Crepis capillaris* give ratios of 15 to 1, but in the one case tested (revolute $\times$ smooth ribs) the type of linkage demanded by such an hypothesis was not obtained. Mating of non-homologous chromosomes should also result in duplication of other genes which should show linkage relations. Although only a small amount of critical data is as yet available, no confirmation of the linkage relations demanded

by these two methods of gene duplication has been obtained. Shull rejected the idea of the occurrence of two independent mutations as a cause of duplication of genes in *Bursa* on the ground that the characters were of such a complex nature that the occurrence of two independent mutations producing identically the same somatic results was on the verge of impossibility. The characters in *Crepis* for which there are duplicate genes cannot be considered as complex, and the occurrence of similar mutations in non-homologous chromosomes therefore seems at the present time to be the more reasonable explanation of the origin of duplicate genes in this species.

Sturtevant (1921) has shown that some points in the germinal material of a given species are more susceptible to mutations than others. There is evidence that such a mutating locus occurs in *capillaris,* for the same character, bald, has appeared in a number of strains derived from widely separated localities. The identity of these genes for bald has been proved in all cases except one (France) by crosses in which they proved to be allelomorphic. That a certain locus may mutate in the same way in other species is at least indicated by the fact that this character is now known to occur in four other species, none of which has been grown extensively among our cultures. The gene for bald is recessive in *capillaris* and is also recessive in the species cross, *setosa* $\times$ *capillaris.*

No less interesting and unique is the group of complementary genes found in *C. capillaris* where the appearance of three such pairs of genes are concerned with the inheritance of leaf characters and a fourth with chlorophyll. It is not strange, however, that a greater number of complex gene relations should be encountered in a species containing a low number of chromosome pairs than in species having a larger number, unless the larger number results from reduplication. There is probably a minimum number of genes which is necessary in any species, and there is no reason to believe, a priori, that a species with a larger number of chromosomes need have a correspondingly larger number of genes. There is also evidence from *Drosophila* that the genes are distributed at random in each chromosome (except in cases of multiple allelomorphs) and among the chromosomes. When this basic number of genes is distributed among a large number of chromosomes, more characters will show simple types of inheritance. When this basic number is distributed in a fewer number of chromosomes, there will necessarily result more complex types of inheritance.

SUMMARY

1. Plants of *Crepis capillaris* are largely cross-fertilized, and this mode of reproduction operates to maintain a condition of genotypic heterozygosity.

2. Inbreeding wild plants thus produced results in the production of a number of pure races which show loss of vigor and reduction in size similar to the effects produced by inbreeding maize.

3. Four sets of duplicate genes are found to be responsible for the inheritance of four different characters. Two of these characters are shown not to be linked. Duplicated genes do not indicate duplicated chromosomes, for each pair is morphologically different from the others.

4. The recessive character 'bald' has appeared in a number of unrelated strains. This is evidence that a certain locus in one chromosome pair mutates more frequently in the same way than do other loci. The appearance of bald in other species may be due to a similar gene in each of these four species.

5. Several types of chlorophyll variations have appeared. Some show monohybrid recessive relations when contrasted with the normal condition, while others show more complex relations.

6. The different forms from widely separated localities show no tendency to approach a common type when grown continuously in the same place.

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EXPLANATION OF PLATES

PLATE 45

Fig. 1. A rosette of the viridis race on the left with a pallid rosette on the right.

Fig. 2. A typical rosette of the scalaris H6 race, showing blunt lobes, ruffled wing on midrib, constricted base of lateral lobes, and a twisting of the lateral lobes.

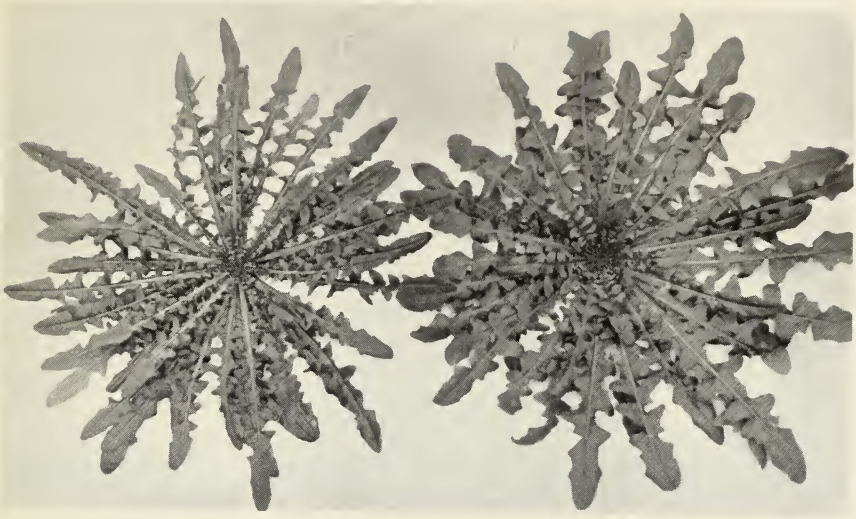


Fig. 1

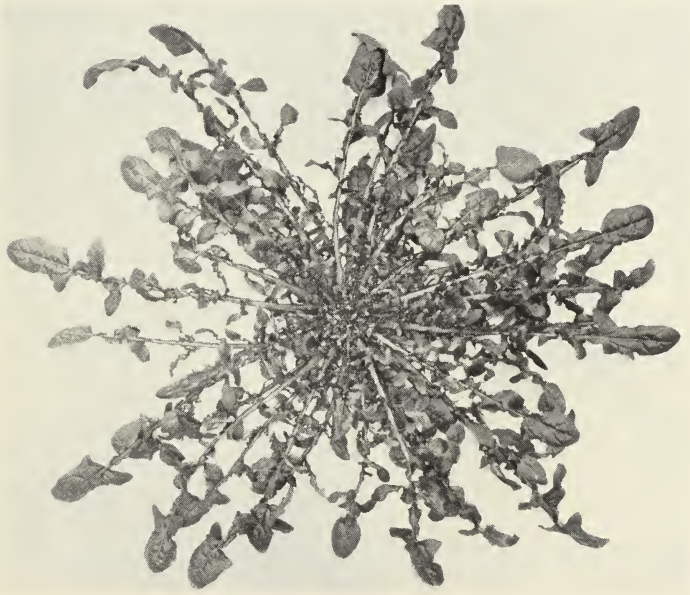


Fig. 2

PLATE 46

Fig. 1. A rosette of simplex Z9 on the left, and at the right the aberrant pinnatifid type which appears in all cultures.

Fig. 2. A rosette of the scalaris e29 race.

Fig. 1

Fig. 2

PLATE 47

Fig. 1. A typical rosette of the pinnatifid leaf, scalaris e28.

Fig. 2. A rosette showing revolute leaves.

Fig. 1

Fig. 2

PLATE 48

Fig. 1. The bicephalic type of fasciation.

Fig. 2. A mature dwarf II plant.

Fig. 1

Fig. 2

PLATE 49

Fig. 1. Two dwarf III plants with two normal sibs.

Fig. 2. A typical plant from the race with the spreading habit.

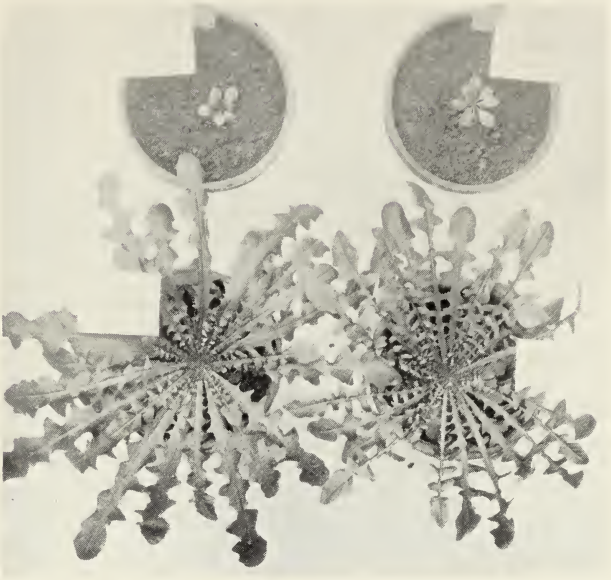


Fig. 1

Fig. 2

PLATE 50

Fig. 1. A typical plant of the erect growth habit.

PLATE 51

Fig. 1. Palea on the left with a receptacle of a normal plant on the right.

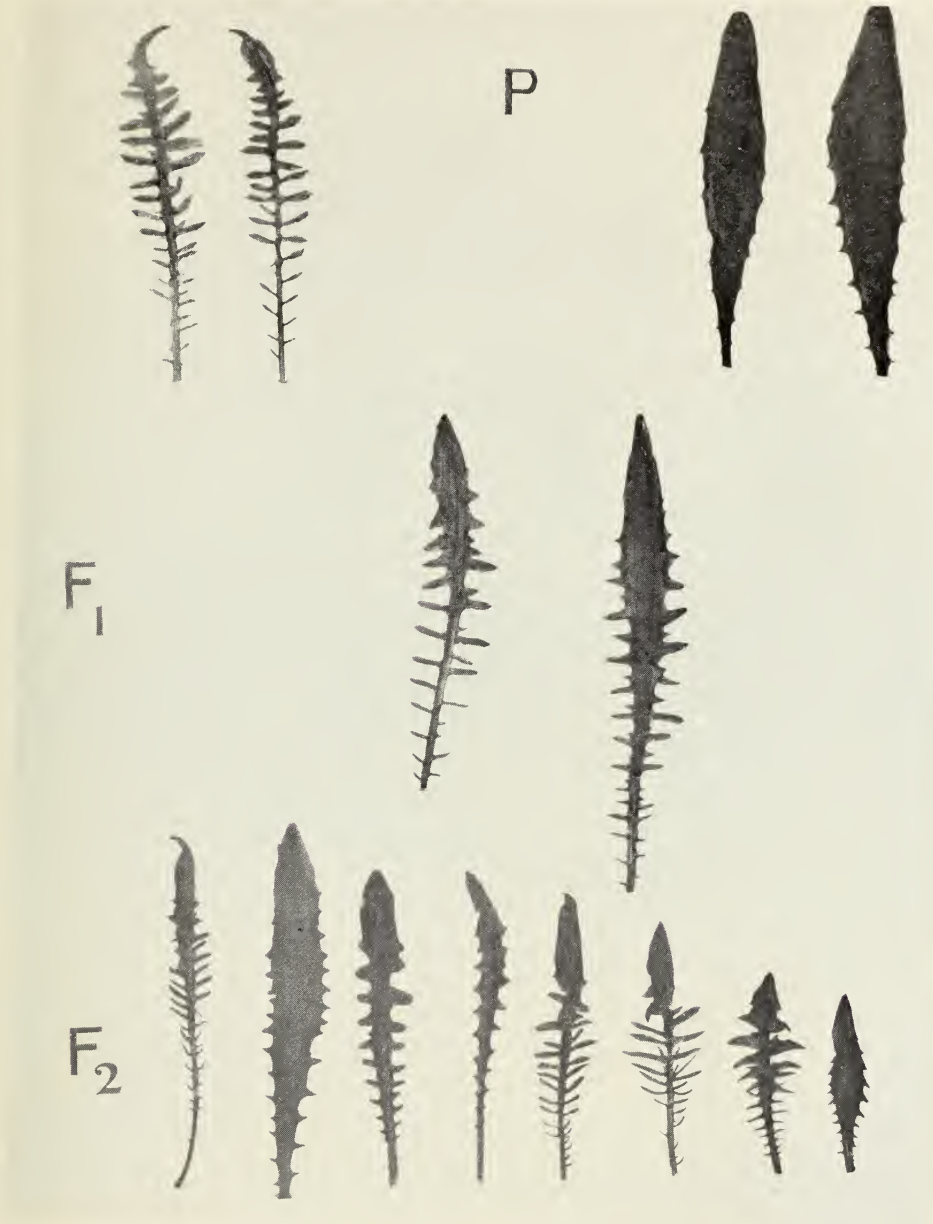
Fig. 2. Three F_2 rosettes from the cross, scalaris $\times$ simplex.

Fig. 1

Fig. 2

PLATE 52

Fig. 1. Typical leaves from two plants of each of the parent strains and of the F_1, together with one leaf from each of eight F_2 plants, which show the results obtained when scalaris and simplex plants are crossed. Note the appearance in F_2 of the curved terminal lobe typical of the scalaris grandparent.


P
F1
F2